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AN INTRODUCTION TO THE REGENERATION OF MALLEE EUCALYPTS

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Abstract

Exploratory studies were conducted on some aspects of the germination and seedling establishment of *Eucalyptus diversifolia, E. incrassata* and *E. oleosa*. Germination was found to be controlled principally by soil moisture and temperature, and soil chemical factors were unimportant. Field germination in 1966 was shown to occur in the autumn-winter period. Seedling establishment appeared to be limited primarily by reduced soil moisture in the spring-summer period. Frost significantly reduced seedling numbers in winter, especially on low-lying sites. Some possible processes by which stands of mallee eucalypts regenerate are discussed.

Introduction

Although mallee eucalypts are frequently observed to recover from burning or felling by the growth of new shoots from the established lignotuber, nothing is known of the factors controlling this process. Mallee eucalypt regeneration from seed is observed occasionally, and this process is also poorly understood. In some areas, seed regeneration is almost invariably destroyed by introduced herbivores, especially rabbits (Zimmer 1940a). The only account of regeneration from seed is that of Zimmer (1940b). On this occasion, seedlings were recorded in December following a fire which destroyed all aerial plant parts the previous January. Regeneration from lignotubers proceeded concurrently with seedling establishment (Zimmer 1940b). The seedling regeneration was of *E. incrassata* Labill. and *E. foecunda* Schau. and rabbits were scarce in the area (W. J. Zimmer, Eastern Hill, Creswick, Victoria; pers. comm.).

This paper reports some short-term exploratory studies on the germination and seedling establishment of the following mallee eucalypts.

(1) *E. diversifolia* Bonpl. This species has a wide edaphic range, and has been found on acidic to neutral deep siliceous sands extremely deficient in all plant nutrients, on highly alkaline deep calcareous beach sands adequately supplied with macronutrients, as well as on a range of nutritionally intermediate soils (Parsons & Specht 1967).

(2) *E. incrassata* Labill. This species is also found on soils with a wide range of pH, calcium carbonate and available nutrient content (Parsons & Specht 1967).

(3) *E. oleosa* F. v. M. ex Miq. This name will be used here to refer to the form of the *E. oleosa* species complex with dull or subglaucous leaves and rostrate operculi, following the work of Mr I. Brooker, Australian National University (pers. comm.). It was previously known as *E. oleosa* var. *glauca* Maiden and *E. transcontinentalis* Maiden. This taxon is found only on alkaline soils containing free calcium carbonate.

All three species are widespread throughout mallee areas in southern Australia (Litchfield 1956).

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Methods and Results

LABORATORY GERMINATION: An experiment was set up

(1) to determine the effect of a range of chemically contrasting mallee topsoils on % germination of the three species, and

(2) to compare the % germination of two populations of *E. diversifolia* from chemically contrasting soils to see if intraspecific differentiation in germination response to soil chemical factors had occurred in this species.

E. oleosa and *E. incrassata* seeds were collected from the field trial site described later. The *E. incrassata* population sampled conformed to the description of *E. incrassata* var. *costata*, which, however, is probably insufficiently distinct to warrant varietal status.

Seeds of *E. diversifolia* from deep siliceous sand (*E. diversifolia* W) and from deep calcareous beach sand (*E. diversifolia* R) were collected from sites at Waitpinga and Robe, South Australia, respectively (see Parsons & Specht 1967).

The soil samples used (Table 1) covered the entire pH and calcium carbonate range of mallee topsoils—from highly alkaline calcareous sand to slightly acidic siliceous sand very low in calcium.

TABLE 1

Soil Sources for the Laboratory Germination Experiment

	Soil Sample (0-1″)		
	D	M	I
Sample description	Calcareous sand	Loamy sand	Siliceous sand
Sample pH	8·3	7·9	6·6
Profile description	Deep calcareous beach sand	Shallow soil on limestone	Duplex sandplain soil
Locality	Robe, S. Aust.	1 mile W. of Tintinara, S. Aust.	Field trial site
Eucalypts present	*E. diversifolia*	*E. diversifolia* *E. incrassata* *E. oleosa*	*E. incrassata*

Equal weights of air-dry soil were added to petri dishes to provide two replicates of each species-soil combination. The soil was maintained in excess of field capacity by watering to 25% moisture content every two days. A control was provided using 'Whatman' seed test circles in petri dishes to provide two replicates per species.

Weighed seed samples were spread evenly over the watered soils in petri dishes on 17 January 1966. The dishes were supplied with light and a constant temperature of 77°F, which are optimal for germination of these species (Grose 1962). Germinations were counted when necessary until the end of the experiment on 24 March 1966, a period of 66 days. Germinates were removed from the dishes when counted.

Although some slight differences in germination rate were found between the various substrates used, these may be caused by small differences in substrate moisture characteristics (Collis-George & Sands 1959), so that rate comparisons between substrates are not relevant here. The number of seeds germinating per weighed sample during 66 days on the seed test circles at 77° F (after which germination has ceased) will be called the laboratory germination capacity. Total germination is expressed as a % of the laboratory germination capacity. At 66 days, occasional germinations of *E. oleosa* and *E. diversifolia* were still occurring on the three soils.

No marked effects of soil type on % germination were found (Table 2). *E. incrassata* seeds had the fastest germination rate on all substrates, and *E. oleosa* the slowest (Fig. 1). There was a marked difference in the fertility of the two *E. diversifolia* seed collections (Table 2), and such intraspecific variability appears to be common in eucalypts (Larsen 1965).

TABLE 2

The Laboratory Germination of Four Populations on Seed Test Circles and Three Soils

Population		Total germination on seed test circles*	% germination on soil		
			D	M	I
E. diversifolia	R	242	100	100	99
E. diversifolia	W	108	94	77	100
E. incrassata		650	85	82	86
E. oleosa		596	76	78	81

* Sums of two replicates

With *E. incrassata* and *E. oleosa*, total germination lower on soils than on seed test circles (Table 2) may be due to seed attack by soil micro-organisms or the presence of some other germination inhibitor in all three soils.

THE FIELD TRIAL: This trial was conducted to investigate germination and seedling establishment of *E. incrassata* and *E. oleosa* under field conditions. In addition, it was hoped that the trial would provide information on the relative performance of these two species on two contrasting soils, one of which was a soil type from which *E. oleosa* is entirely absent in the field.

The trial was conducted in the Ninety Mile Plain, South Australia, where detailed information on soils and vegetation was already available.

An area was chosen in a strip of mallee surveyed as a road between Sections 10 and 11, Hundred of Cannawigara, which was mature and relatively undisturbed except for an access track. The soils and climate of this area have been described by Blackburn *et al.* (1953) and the vegetation by Litchfield (1956). The area chosen provided two distinct soil associations carrying different combinations of eucalypts in a small area. Plots were set up on both soil associations.

(1) *The Willyama association.* The well drained parts of the Willyama association in this area carry a stand of mallee dominated by *E. incrassata* and *E. oleosa*, with some *E. foecunda* and an understory dominated by *Melaleuca uncinata*.

The soil profile is as follows:

0–4 in.	Light brown sand.
4–20 in.	Yellowish brown sandy clay with few lime nodules.
20–62 in.	Yellowish brown sandy clay, with much lime in hard and soft states. In places the profile is entirely hard and soft lime from 20 in. onwards.

This profile is typical of the shallow duplex soils on limestone plains in the Ninety Mile Plain, and they usually carry this assemblage of eucalypts. The site on this soil (which is referred to as the *E. oleosa* site) was the seed source for both species.

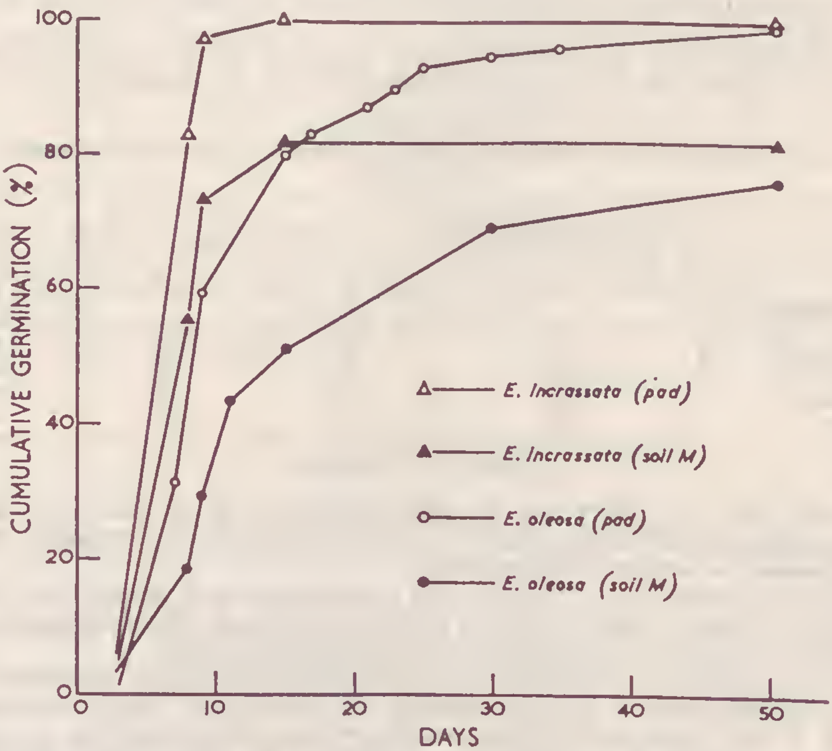

FIG. 1—Germination rates of two species on seed test circles ('pad') and soil M.

(2) *The Buckingham association.* These soils occurred one mile E. of, and at a slightly higher altitude than, the Willyama association. In this area they carry *E. incrassata* with less *E. foecunda* over *Melaleuca uncinata*. The plots were set up on a soil with the following profile:

0–12 in.	Greyish-brown sand.
12–18 in.	Tough columnar mottled yellowish brown, brown and grey sandy clay.
18–33 in.	Mottled yellowish brown and brownish yellow sandy clay.
33–38 in.	As above with a few flecks of soft lime.

This is a duplex sandplain soil with tough clay subsoil typical of the duplex soils carrying *E. incrassata* throughout the Ninety Mile Plain. *E. oleosa* is invariably absent from such soils. This site is referred to as the *E. incrassata* site.

At each site, two 59 sq. ft plots were selected in relatively open parts of the community (so that large lignotubers were absent), were cleared of aerial plant parts and litter, and fenced against rabbits. Large shoots were removed for 6 ft around each plot to minimize variation in shading effects between plots. Within each fenced plot were two seed beds, each 15 sq. ft in area, two seedling beds, each 3 sq. ft in area, and an access path through the middle of the plot, containing a rain gauge.

Seeds and seedlings were planted at four intervals between 24 April 1965 and 13 September 1965 in one randomly chosen seed bed and seedling bed. Observations continued until 1966. At each planting, one seed bed at each site was sown with a seed mixture containing 2·0 g of *E. incrassata* seed and 1·0 g of *E. oleosa* seed (chaff removed by sieving in both cases).

A seed mixture was used so that the environments for seedlings of each species would be as similar as possible, and to include the possibility of interaction between seedlings of the two species in the experimental design.

The seed was covered with a thin ($\frac{1}{8}$-$\frac{1}{4}$ in.) layer of topsoil after broadcasting, to minimize harvesting by ants. Germination tests in a 77°F constant-temperature room both before the first planting and after the last planting showed no appreciable change in the fertility of the seed lots with time, and established that the 1·0 g–2·0 g mixture contained 1120 fertile seeds of *E. oleosa* and 1150 fertile seeds of *E. incrassata*.

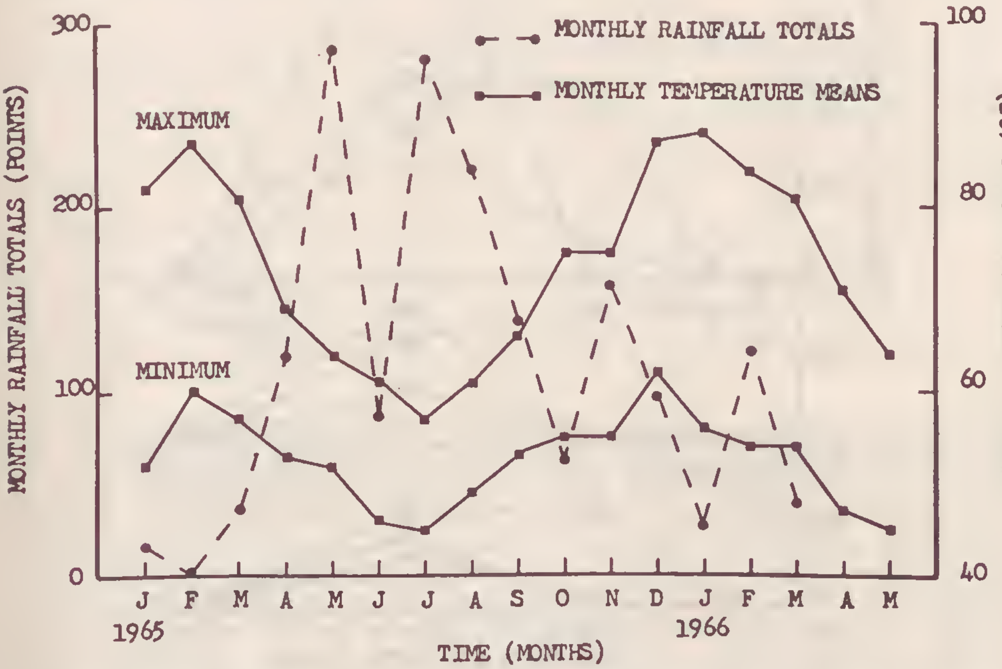

FIG. 2—Monthly meteorological data recorded during the field trial by stations nearby.

Seedlings were transplanted in the field ten days after germination (when their root systems were 2–3 in. long), and were washed free of soil before transplanting. Ten seedlings were transplanted at each site at every planting.

Rainfall data only were recorded at the experimental sites—temperature data are taken from the Keith Meteorological Station, approximately 15 miles E., and monthly rainfall data from Wirrega (Fig. 2), 5 miles SW.

The seedling beds were used as controls to check on germination of the two eucalypts from natural seed fall. No such germination was recorded at any time.

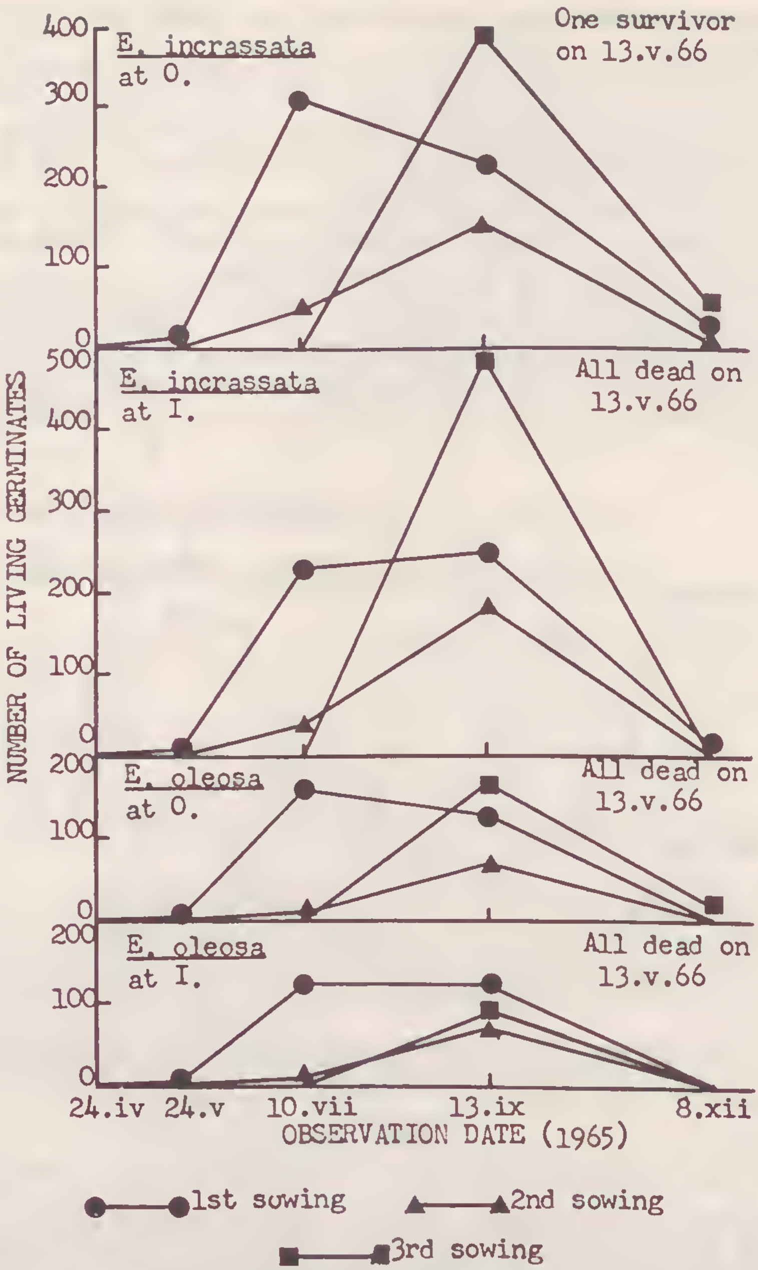

FIG. 3—The number of living germinates present in the plots from three successive sowings of mixed seed of two species on two soils. O = *E. oleosa* site, I = *E. incrassata* site. All seeds sown on 13/ix/65 failed to germinate.

The trial was commenced on 24 April 1965, and concluded on 13 May 1966, when road-building operations to a newly developed quarry destroyed half the plots.

(a) *Results of the seed sowing experiment.*

The results of this experiment are summarized in Fig. 3. Field germination is expressed as a % of laboratory germination capacity. As field germination was determined from the emergence of the cotyledons from the soil, no data on pre-emergence deaths were obtained and all germination figures represent net germination only.

The rainfall observations showed that rainfall was closely comparable at the two sites.

TABLE 3

Winter Deaths of Germinates as a % of the Total Number of Germinates; and Number of Delayed Germinations recorded in the Second Autumn of the Experiment
I = *E. incrassata*; O = *E. oleosa*

Sowing date	Site	Winter deaths (%) of each species (all recorded on 13.ix.65)		Delayed germinations of each species (all recorded on 13.v.66)	
		O	I	O	I
24.iv.65	O	11	17	7	–
	I	—	2	–	–
24.v.65	O	16	27	4	–
	I	6	5	–	–
10.vii.65	O	—	—	2	–
	I	—	—	–	–
13.ix.65	O	—	—	1	–
	I	—	—	–	–

(1) *Germination*: Germination for both species occurred throughout the period May to at least July, the period of greatest soil moisture. All total germinations for the late May sowing were lower than the totals from both the late April sowing and the July sowing (Fig. 3). This reduction of germination was much more marked on the low-lying *E. oleosa* site. The two months following the May sowing were colder than the two months following the other two sowings (Fig. 2), so that the available data suggest a depressing effect of low temperature on germination or pre-emergence seedling survival. The September sowing completely failed to germinate, almost certainly as a result of low rainfall and therefore dry soil conditions in this period (Fig. 2). However, germination may occur in spring in wetter years than 1965, which had a spring rainfall considerably below average (spring rainfall 1965 = 356 points, mean spring rainfall = 578 points).

Maximum germination in the plots varied from 7% to 44% of the laboratory germination capacity. In similar studies, but without a protective soil covering on the seeds, Florence (1961) recorded a range from 3% to 34% for *E. pilularis* Sm. and Cunningham (1960) a range from 8% to 12% for *E. regnans* F.v.M.

Percentage germination of *E. incrassata* was much greater than that for *E. oleosa* at both sites for all plantings (mean % germination of *E. incrassata* for all sowings = 27%; of *E. oleosa* = 10%).

The germination of each species was similar on the two soils studied, in agreement with the laboratory study.

When the plots were inspected in May 1966, following autumn rains, some new germination was observed at the *E. oleosa* site on the plots sown in April, May and July 1965 (Table 3). This delayed germination was all of *E. oleosa.*

(2) *Establishment and survival of germinates*: In general, seedling numbers reached a maximum two to four months from sowing, and then showed a very marked decline with the onset of drier soil conditions and higher temperatures in late spring and early summer (Fig. 3). In addition, the September plot inspection revealed a number of dead seedlings (Table 3) at a time when rainfall records and soil inspection at both sites showed that soil moisture was optimal. The period between the July inspection, when no deaths were apparent, and the September inspection coincided with the period of most severe frosts in the area, when three daily minimum screen temperatures below 29·5°F were recorded at Keith. This suggests that the deaths were caused by frost, and this hypothesis is supported by the following observations: (a) Death percentages were much higher at the low-lying *E. oleosa* site, where lower temperatures caused by cold air drainage would be expected. Comparative daily ground-level temperature observations at the two sites in May 1966 showed that the *E. oleosa* site was 4-6°F colder than the *E. incrassata* site. (b) No symptoms of 'damping-off' or other fungal infections were observed on either dead or damaged seedlings.

The winter deaths observed were all of seedlings from the April and May sowing. It appears that the seeds sown later were prevented from germinating by the cold July-early August weather, and germinated in the warmer weather of late August, thereby escaping frost damage.

By December, almost all the seedlings were found to be dead. These losses coincided with dry soil conditions caused by low rainfall and high temperatures (Fig. 2). The losses then, are most likely to be due to drought and possibly also to lethal temperatures on the hypocotyl at the soil-air junction (Cunningham 1960). By May 1966 only one seedling remained alive. This seedling, of *E. incrassata*, was 2·5 cm high and at the four-leaf stage.

(b) *The results of the seedling transplant experiment.*

The seedlings transplanted in late April had all died by May, reflecting the low levels of soil moisture in the first part of this period. Otherwise the pattern of survival was similar to that of the seedlings from the sowing experiment, with some winter losses suggesting death by frost, and the death of the remaining seedlings during the summer drought.

Discussion

The laboratory germination experiment showed that soil chemical properties do not appear to exert significant effects on the germination of the four populations examined; if such properties influence the distribution of the three species, they must do so at later stages of the life cycle.

This finding contrasts with the marked inter- and intra-specific differentiation in germination response to these factors shown elsewhere (Mayer & Poljakoff-Mayber 1963, Ramakrishnan 1965).

E. incrassata seeds are completely non-dormant (Larsen 1965), and this behaviour explains the absence of delayed germination in the field (Table 3). By contrast, *E. oleosa* seeds are rated as 'dormant' by Larsen (1965) and they show delayed germination in the field. The slower germination rate (Fig. 1) and lower field germination capacity (Fig. 3) recorded for *E. oleosa* are probably related to this dormant behaviour.

The ecological significance of these differences in dormancy needs to be assessed in a long-term study of regeneration from seed covering a range of climatic regimes, and in conjunction with studies on the relative seed production of the two species. It is possible that the dormancy of *E. oleosa* seeds is one of the factors enabling *E. oleosa* to establish in drier areas than *E. incrassata*.

The observations of Zimmer (1940b) established that natural regeneration of mallee eucalypts from seed can occur following the marked reduction of community transpiration caused by bush fires. However, it is probable that competition for water from the faster-growing lignotuber regeneration would be lethal for at least some of the seedlings.

In the present study, although aerial plant parts were removed from the plots themselves, many roots from actively transpiring plants nearby were certainly present. Under these conditions, and in the climate prevailing during the study, survival of seedlings through the summer was negligible, the principal limiting factor being the dry spring and summer climate. However, these results apply only to years of sub-average spring rainfall like 1965, and seedling establishment may have been significant if rainfall had been average or above average. Elsey (1957) reached similar conclusions in his study of *Callitris* regeneration in the Warby Ranges, where spring and summer rainfall is again the principal determinant of seedling survival in the first year. He recorded a year of sub-average August-October rainfall which killed all *Callitris* germinates of that year, occurring between two years of above average August-October rainfall in which plentiful seedling establishment occurred. Elsey (1957) also found that seedlings that survived the first summer were seldom killed by drought in the second or later years.

Seedling establishment in gaps in a mature stand, such as in the plots of the present study, may exist as small lignotuberous advance growth (Jacobs 1955) until death of the mature trees makes water available for more rapid growth. Such an establishment pattern has been demonstrated in *E. marginata* stands by van Noort (1960), where such lignotuberous advance growth may exist in a 'dormant' phase beneath mature forest for more than 20 years.

In the case of destruction of the aerial parts of mature mallee stands by fire, regeneration from lignotubers has a marked advantage over seedling regeneration. In the present study, some mature mallee stems were cut down while erecting the plots. The remaining lignotubers produced new shoots in spring 1965. In May 1966 these shoots were up to 32 cm long and each shoot carried up to 11 large leaves, while the surviving seedling was only 2·5 cm high with 4 very small leaves. This suggests that the regrowth from the lignotubers will kill or suppress seedling regeneration which may only establish in gaps formed when degenerate lignotubers rot and die. If degenerate lignotubers are simultaneously killed by fire, then an even-aged crop of seedlings may become established.

Another aspect requiring investigation is the age at which mallee eucalypts first produce seeds. On 23 November 1959 fire destroyed all aerial parts of a stand of *E. incrassata* and *E. foecunda* in Wyperfeld National Park. When examined on 15 July 1967 lignotuber regeneration of both species was carrying what appeared to be the first crop of fruits since the fire (R. Campbell, Yaapeet, pers. comm.). No data are available on time from germination to production of first fruit crop.

Clearly, long-term studies with more replication than was possible in the present work are needed to investigate thoroughly the biology of mallee eucalypts and many other native plant species.

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